# 3. Environmental Studies on the Limpet. By E. S. Russell, M.A.\*

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(Text-figures 217-228.)

#### Introduction.

The object of this paper is to correlate certain modifications of the shell of Patella vulgata with definite environmental conditions. Patella is stationary; hence if one takes a number of shells from one locality and contrasts them with a number from another locality, which differs from the first in certain definite respects, any differences between the two sets may be safely put down to the influence of the environmental factors in which the localities differ. That is true if there has been no selective process at work, and since the differences found were slight and apparently of no selective value I have assumed the absence of selection. Measurements were made of several hundred shells from definite localities and the ratios of the dimensions calculated. Since the ratios of length to breadth  $\binom{L}{B}$ , length to height  $\binom{L}{H}$ , and distance from apex to posterior edge to distance from apex to anterior edge  $\binom{Ab}{Af}$  change very rapidly with the growth of the shell, it has been necessary to arrange the ratios in groups according to the size of shell, and to calculate the mean values for each group separately.

The shells measured were collected in 1903 and 1904 at W. Bennan, Arran. A few shells of *P. athletica* were included.

I desire to express my indebtedness to Dr. J. F. Gemmill, Glasgow University, whose interesting papers on sex in the Limpet are well known, for much helpful criticism.

I hope to work out from my data on a future occasion some results concerning variation, laws of growth, and correlation in the shell of *Patella*.

# I. The Homing Habit of the Limpet.

It has long been matter of common knowledge that a limpet, when once it has taken up a fixed position on a rock, only leaves that position to make short excursions for food, and returns always to it. This fact may be taken as well established.

Most of the published observations, however, concerning this habit of the limpet record merely isolated cases, and many gaps remain in our knowledge of it.

There is no agreement among authors as to the time at which the limpet leaves its "home" to seek for food. Lukis (10), Jeffreys (9), Peach (quoted by Jeffreys), and Robertson (14) state that the limpet wanders when covered by the tide. Davis (3) and H. Fischer (6) state that it wanders while uncovered, and

<sup>\*</sup> Communicated by the SECRETARY.

P. Fischer (7) says that young ones wander only when uncovered. Bouchard-Chantereaux (1) says that it makes its excursions just after the tide goes out, Lloyd Morgan (11) that it wanders chiefly as the tide leaves it, and as the tide returns. Lloyd Morgan and Roberts (13) are of opinion that it does not move about when submerged.

The observations recorded in this paper show that limpets above 20 mm. or so in length do not wander when uncovered by the tide. Smaller limpets, however, may wander even when uncovered, but also when they are covered by the tide. I believe that the differences of opinion regarding this point arise from the fact that the habit of fixity becomes established only when the shell has reached a length of 10–15 mm. Dr. Robertson's observations seem to me to be the fullest and most satisfactory of all. He found that limpets go out on the flow of the tide, sometimes for two consecutive tides, sometimes alternately. Limpets in captivity had very much the same habits, going out to browse about once in the twelve hours.

The greatest distance from which a limpet has been known to return to its "home" is three feet (Davis, 3).

The seat of the limpet's marvellous sense of direction is quite unknown, and the accuracy with which it returns to a definite spot is very astonishing. Several observers (Lukis, Roberts, Hawkshaw, Robertson, Morgan) have noticed that the edge of the shell is often accurately adjusted to the irregularities of the rock, or to barnacles, round about the "home." I have recorded in this paper one or two other instances of the same thing.

As to how long a limpet may stay in one spot, Lukis records the fact that five limpets observed in 1829 were found in the same position several months after; and I have had one or two under observation for six months which kept exactly to the same spot.

I give here some observations made in 1906 at Kames, Kyles of Bute, on a number of limpets in their natural habitat. Each of the limpets had a distinctive mark filed on its shell, so that no mistake as to identity might be made. All the measurements were taken while the limpets were uncovered by the tide. The first table refers to four limpets, ranging in size from 34 mm. to 44 mm., which grew close together on a ledge of rock near high-water mark.

TABLE I.

| Distances<br>apart<br>(in mm.). | 30th June. | 3rd July. | 10th July. | 26th July. | 30th July.        |
|---------------------------------|------------|-----------|------------|------------|-------------------|
| 1 and 2                         | 42         | 41        | 42         | 41         | 41                |
| 2 and 3                         | 65         | 65        | 65         | 64.5       | 64.2              |
| 3 and 4                         | 35         | 34        | 35         | 36         | 35                |
| 4 and 1                         | 75         | 76        | 74.5       | 75         | 75 <sup>.</sup> 5 |

During a whole month, therefore, the relative positions of these limpets remained practically unchanged. One of them, No. 3, was almost surrounded by barnacles, to which its shell fitted

accurately.

The relative positions of another series of limpets for various dates during a month are given in Table II. The sizes ranged from 8.5 mm. to 34 mm. The stone on which they were lay near low-water mark, and was largely overgrown with *Fucus*.

TABLE II.

| Distances apart (in mm.). | 30th June. | 7th July. | 10th July. | 26th July. | 30th July. |
|---------------------------|------------|-----------|------------|------------|------------|
| 1 and 2                   | 29         | •••       | 30 ·       | 80         | 65         |
| 1 and 3                   | 44         |           | 44         | 42.5       | 44.5       |
| 3 and 4                   | 87         |           | 87.5       | 92         | 88         |
| 4 and 5                   | 49         | 65        | (46), 49   | 46.5       | 46         |
| 5 and 6                   | 98         | •••       | (90), 98   | 97.5       | 102        |
| 7 and 8                   | 4th July.  | 50        | 19         |            | 300        |

At first sight these data seem contradictory of those in Table I., but the inconsistencies can be easily explained. The limpets in Table I. are all large; in Table II. only Nos. 1, 3, and 4 are more than 30 mm. long. The relative positions of Nos. 1, 3, and 4 are very constant. No. 2 in Table II. is a limpet 8.5 mm. in length, and the great variation of its distance from No. 1 (30.5 mm. long) covers the fact that No. 2 wandered, while No. 1 was quite stationary. Nos. 7 and 8 are small limpets—both under 15 mm. —and both wandered a good deal. Nos. 5 and 6 are limpets 20 mm, and 24 mm, long respectively, and their relative distance (and also No. 5's distance from No. 4) shows on the whole quite small variations. The greatest variation of No. 5's distance from No. 4 is that given under date 7th July, when the distance was 65 mm, as against the usual 49 mm. On this occasion it was No. 5 which had moved, while No. 4 had not changed its position.

The conclusion may be drawn therefore that large limpets are more fixed in their position than small limpets. It will be noticed that double measurements are given for the distances of Nos. 4 and 5, and 5 and 6, under the date 10th July, and further, that the second measurement in each case is the same as that made on the 30th June. The explanation is rather interesting. On 10th July the first measurements (those in brackets) had just been made

when I noticed that No. 5 was moving. Nos. 4 and 6 made no movement. No. 5 crept a few millimetres, and fitted the indentations of the hinder edge of its shell to three barnacles adhering to the stone. It then settled down as if for good, and moved no more. On re-measuring its distances from No. 4 and No. 6, I found them to be identical with the distances measured on 30th June. Evidently the positions of No. 4 and 6 were definitely fixed, and No. 5, too, had a definitely fixed place of abode and was able to find its way back thereto with astonishing accuracy.

On the 26th and 30th July I noticed that the weed growing on the stone had covered over most of the limpets and so kept them moist. I believe that under these circumstances the limpets, especially the small ones, moved about a little more than usual, and did not return so carefully to their fixed positions. The figures certainly show considerable variations for these dates.

I kept records also of the movements of five small limpets, a (10) mm.), b (13 mm.), c (4 mm.), d (7 mm.), and e (5.5 mm.). They were under observation at intervals for over three weeks. records may be summarised as follows:—a was to be found always within a few centimetres of one fixed spot, and on the 11th, 12th, and 30th July was found on that spot, with its shell fitted to a Spirorbis-tube and to a barnacle. On the 30th July I saw it move to the spot and adjust itself. Limpet b was more irregular, and did not seem to have a fixed stance, but it was always to be found near at hand. Limpet c changed its position by a few centimetres from time to time. Limpets d and e occupied on 5th July a definite position on a clearly marked circular space on a stone. On the 10th, 11th, 26th, and 30th of the same month they occupied exactly the same positions. On the 7th they were distant 4 cm. and 8 cm., evidently in search of food. On the 12th, at 9.30 A.M., e was in position, d 3 cm. away. The stone had just been uncovered, and  $\tilde{d}$  was on its way "home." Twenty minutes later I found d in position. These two limpets therefore had a definite home, to which they returned when the tide left them high and dry.

A well-known fact which goes far to prove the homing habit of *Patella* may here be mentioned. One may often find on the shore a limpet quite surrounded and hemmed in with barnacles. If one knocks the limpet off one finds a clear space on the rock below, the outline of which, formed by the barnacles, closely follows that of the limpet's shell. Another fact of the same kind may often be observed. If a large limpet adhering to a smooth surface of rock be detached, a dark "weathering," of shape corresponding

to the limpet's, will usually be seen.

The former of these facts affords a simple method of determining the size at which a limpet settles down to a fixed abode. I have not seen any below 10 mm. in length occupying a definite position marked out by barnacles. Near low-water mark the average size at which limpets settle down seems to be, as determined by this method, about 15 mm., though I have seen

several fixed from 10-12 mm. long. Davis (4) found a limpet

 $\frac{17}{30}$  inch long homing, and also smaller ones.

From all these observations, then, the following conclusions can be drawn:—(1) that every limpet of 15 mm. and upwards occupies, for long periods at a time, a definitely fixed position, to which it returns after any wanderings that it may make for food; (2) that limpets under 15 mm., if not yet settled in a definite position, at least never wander far away, and so generally keep to the same stone; (3) that limpets wander chiefly when covered by the tide.

In many cases, of course, the limpet settles down at a much smaller size than 15 mm.—for example, a at 10 mm., d at 7 mm., and e at 5.5 mm. The factors delaying fixation would seem to be three: 1st, a short exposure to air; 2nd, the moisture and shelter afforded by weed; 3rd, want of a suitable place for settling down. The late fixation of low-water limpets is undoubtedly due to the first two causes, which usually act in conjunction with one another. The third factor comes into play in the case where a small limpet establishes itself on a stone which is completely covered with barnacles, and can find no uncovered patch of rock on which to settle down.

### II. High-water and Low-water Limpets.

Table III. gives the average ratios for 300 limpets collected at two different stations near high-water mark, 200 at Station 1, and 100 at Station 2.

Table III.

High-water Limpets.

| Size.    | No.<br>measured. | $\frac{\mathrm{L}}{\mathrm{B}}$ . | $\frac{Ab}{Af}$ . | H.<br>T | $\frac{B}{B}$ . |
|----------|------------------|-----------------------------------|-------------------|---------|-----------------|
| 5—10 mm. | 6                | 1.25                              | 1.28              | 3.86    | •324            |
| 1015 ,,  | 30               | 1.28                              | 1.52              | 3.67    | ·349            |
| 15—20 ,, | 64               | 1.24                              | 1:42              | 3.44    | .360            |
| 20-25 ,, | 21               | 1.25                              | 1.45              | 3.19    | 392             |
| 25-30 ,, | 13               | 1.22                              | 1.34              | 2.95    | 414             |
| 30-35 ,, | 11               | 1.21                              | 1.39              | 2.73    | .443            |
| 35-40 ,, | 16               | 1.18                              | 1.28              | 2.53    | '466            |
| 40-45 ,, | 29               | 1.16                              | 1.29              | 2.30    | 504             |
| 4550 ,,  | 55               | 1.15                              | 1.26              | 2.18    | *528            |
| 50-55 ,, | 47               | 1.15                              | 1.22              | 2.04    | •564            |
| 55-60 ,, | 7                | 1.15                              | 1.19              | 2.05    | .561            |
| 60-65 ,, | 1                | 1.15                              | 1.27              | 2.21    | .520            |

Table IV. gives the average ratios of a like number of shells collected—200 at Station 1, 100 at Station 2—at low water.

| TABLE     | IV.      |
|-----------|----------|
| Low-water | Limpets. |

| Size.    | No. | F.   | $\frac{\mathrm{Ab}}{\mathrm{Af}}$ . | $\frac{\mathrm{L}}{\mathrm{H}}$ . | $\frac{\mathrm{H}}{\mathrm{B}}$ . |
|----------|-----|------|-------------------------------------|-----------------------------------|-----------------------------------|
| 0— 5 mm. | 1   | 1.33 | 1.20                                | 3:33                              | •399                              |
| 5—10 ,,  | 15  | 1.34 | 1.67                                | 3.45                              | *388                              |
| 10-15 ,, | 51  | 1.29 | 1.60                                | 3.85                              | ·335                              |
| 15-20 ,, | 53  | 1.28 | 1.21                                | 3.61                              | *355                              |
| 20-25 ,, | 36  | 1.25 | 1.44                                | 3.67                              | ·341                              |
| 25-30    | 29  | 1.23 | 1.37                                | 3.31                              | ·372                              |
| 30-35 ,, | 29  | 1.21 | 1.34                                | 3.11                              | .389                              |
| 35—40 ,, | 20  | 1.19 | 1.33                                | 3.02                              | •390                              |
| 40-45 ,, | 27  | 1.17 | 1.26                                | 2.86                              | •409                              |
| 45-50 ,, | 18  | 1.17 | 1.24                                | 2.77                              | .422                              |
| 50—55 "  | 11  | 1.16 | 1.16                                | 2.59                              | •448                              |
| EE 60    | 7   | 1.15 | 1.19                                | 2.67                              | .431                              |
| 00 07    | 2   | 1.18 | 1.11                                | 2.36                              | .500                              |
| 65—70 ,, | ĩ   | 1.18 | 1.48                                | 2.75                              | •429                              |
| . , ,    | -   |      |                                     |                                   |                                   |

In considering the differences between the two sets of shells only those between 10 mm, and 55 mm, in length will be taken into account, since those below 10 mm, and above 55 mm, are too few to give smooth results.

 $\frac{L}{B}$ .—This ratio is greater in low-water than in high-water shells for every stage except two, viz. 20–25 mm. and 30–35 mm., where it is the same in both. High-water shells are therefore at almost every stage a little broader than low-water shells.

 $\frac{\text{Ab}}{\text{Af}}$ .—This ratio is on the whole greater in low-water shells up to about 40 mm., when it becomes smaller in the low-water than in the high-water shells. The apex would seem therefore to be further forward in low-water shells up to 40 mm. in length and thereafter further back than in high-water shells.

 $\frac{L}{H}$ .—The high-water limpets are at all stages higher spired than the low-water limpets.

H.—The high-water shells are at all stages narrower in proportion to their height.

As to the causes of these differences, one can say little more than that they must be due to those factors in which a high-water environment differs from a low-water environment. Size of High-water Limpets.—It seems to be the opinion of most authorities that high-water limpets are on the whole smaller

than low-water limpets.

Canon Norman (12) says definitely:—"It will be found to be a general rule with regard to the Limpet, that the nearer highwater mark the shells are taken, the higher spired, more strongly ribbed, and smaller it will be; and that the lower down it lives, the flatter, less ribbed, and larger it becomes." While my observations entirely corroborate the truth of the statement that highwater limpets are typically high-spired, yet I find, for one area at least, that the proportion of large shells is greater at highwater than at low-water. Table III. shows that of 300 high-water limpets collected without conscious preference of large over small, 161, or 532 per cent., were under 40 mm. in length, and 139, or  $46\frac{1}{3}$  per cent., were over 40 mm. From Table IV. it appears that 234, or 78 per cent., of the low-water shells were below 40 mm., and only 66 or 22 per cent. were above 40 mm. in length. The average maximal size of the high-water shells is about 55 mm., of the low-water shells about 50 mm. For the locality therefore in which these limpets were collected, the proportion of large limpets was considerably greater at highwater than at low-water.

Of course that does not mean that here and there a low-water limpet may not be found as large as, or larger than, any high-water limpet. As a matter of fact, of the six specimens over 60 mm. long which I obtained among the 1000 collected, three came from high-water, and three from low-water level; and the largest of these, a limpet 66 mm. long, came from low-water level.

# III. Sheltered and Exposed Limpets.

Table V. gives the mean ratios of 100 limpets collected from sheltered situations in one definite locality, and of 100 limpets collected from exposed situations in the same locality.

Table V.
Sheltered. Exposed.

| Size.  | L<br>B·  | $\frac{\mathrm{Ab}}{\mathrm{Af}}$ .                                  | H.   | $\frac{\overline{B}}{\Gamma}$                                | $\frac{Ab}{Af}$ .  | L<br>H   |
|--|--|--|--|--|--|--|
| 10—15 mm. 15—20 ,, 20—25 ,, 25—30 ,, 30—35 ,, 35—40 ,, 40—45 ,, 45—50 ,, | 1.25<br>1.23<br>1.23<br>1.16<br>1.16<br>1.15<br>1.16 | 1 46<br>1 41<br>1 44<br>1 39<br>1 35<br>1 34<br>1 29<br>1 23<br>1 25 | 3:38<br>3:08<br>5:13<br>2:84<br>2:62<br>2:37<br>2:22<br>2:07<br>2:07 | 1·32<br>1·31<br>1·28<br>1·23<br>1·23<br>1·21<br>1·18<br>1·16 | 1:49<br>1:49<br>1:34<br>1:41<br>1:30<br>1:34<br>1:23<br>1:18 | 2·75<br>3·12<br>2·83<br>3·02<br>2·49<br>2·50<br>2·28<br>2·25 |
| 50—55 ,,<br>55—60 ,,   | 1·15<br>1·16   | 1.16   | 2.00   | 1.12   | 1.13   | 2·19<br>2·29   |

Table VI. gives ratios for a series of 100 exposed shells from another locality.

Table VI.
Exposed Limpets.

| Size.   | $\frac{\mathbf{L}}{\mathbf{B}}$              | $\frac{\mathrm{Ab}}{\mathrm{Af}}$ .                  | L<br>H   |
|---|--|--|--|
| 10—15 mm.<br>15—20 ,,<br>20—25 ,,<br>25—30 ,,<br>30—35 ,,<br>35—40 ,,<br>40—45 ,, | 1·27<br>1·33<br>1·25<br>1·26<br>1·22<br>1·21 | 1·59<br>1·47<br>1·47<br>1·38<br>1·28<br>1·35<br>1·29 | 3·26<br>3·33<br>3·00<br>2·75<br>2·72<br>2·49<br>2·48 |
| 45—50 ,,<br>50—55 ,,<br>55—60 ,,  | 1·17<br>1·17<br>1·15                         | 1·27<br>1·28<br>1·22                                 | 2·37<br>2·25<br>2·18                                 |

The numbers measured are rather small to give very definite results; and the distinction between sheltered and exposed limpets is a little arbitrary. Shells which were attached to the under side of stones, or to the side nearest the shore, or which lurked in nooks and crevices, were taken to be sheltered; while shells attached to the upper side, or to the side nearest the sea, were considered to be exposed.

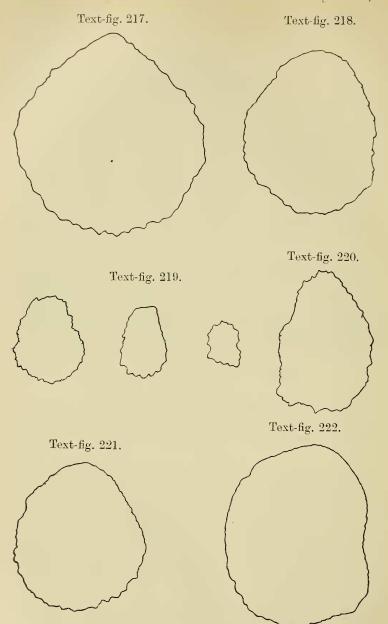
 $\frac{L}{B}$ .—The exposed shells are on the whole narrower than the sheltered shells.

 $\frac{Ab}{Af}$ .—No definite conclusion can be drawn from the differences shown by this series.

 $\frac{L}{H}$ .—Comparison of the ratios for shells below 30 mm. gives conflicting results. For shells above 30 mm., however, this ratio is distinctly greater in both sets of exposed shells than in the sheltered set. Exposed shells of 30 mm. and upward are therefore lower than sheltered shells of corresponding length.

The fact that the decrease in height becomes apparent only in large shells leads one to think that the decrease is due to the greater erosion to which exposed shells are necessarily subject. The differences between the two sets of shells must be explained as the direct result of the difference in the amount of friction to which they are respectively subjected.

These observations partly bear out and partly contradict the statement made by Davis and Fleure (5) that the shells of limpets



Text-figs. 217-222.—Some irregular outlines, all of exposed shells.

on exposed flat surfaces are typically low and broad, and that shells on sheltered surfaces are typically high and narrow.

The results obtained by Cooke (2) for shells of Purpura lapillus may be recalled here. He found that shells in exposed places were stunted and had a large mouth, and that shells in sheltered spots were large and possessed a well-developed spire and a small mouth. With regard to stunting, I find that a larger proportion, namely 55 per cent., of the exposed shells are below 40 mm. in length, than in the case of the sheltered shells, where the proportion is 34 per cent. This fact may point to some stunting among the exposed shells, but many exposed shells reach a great size.

Two other points of difference between exposed and sheltered limpets, and perhaps more important ones, become evident when a number of exposed shells are directly compared with a number of sheltered shells. Exposed shells are typically thick and heavy. This thickness of the shell is probably a direct adaptation to the greater shocks which an exposed shell has to withstand. The second difference is that exposed shells are much more irregular in outline than sheltered shells. Of the shells which I kept on account of their irregular outline, the majority came from exposed limpets, and the outlines selected for illustration (text-figs. 217-222) are all drawn from exposed shells. On the other hand, the most beautiful symmetrical shells to be got are those which one finds on the smooth under surface of a stone in a rock-pool. i.e. in a very sheltered situation. It is natural that exposed limpets should fit their shells to the irregularities of the rock to which they cling, in order to gain support against the waves and tide, and that (as will be shown in the next section) their shells should for this reason grow irregular in outline.

To sum up, adult exposed shells of *Patella* are lower spired, narrower, thicker, and more irregular in outline than sheltered shells; and these differences are probably due to the difference of friction to which the two kinds of shells are exposed from waves

and tide.

## IV. Limpets on Rough Stones and Limpets on Smooth Stones.

While I was collecting limpets for measurement at the Southend of Arran I noticed that they were of two distinct types, a "rough" type and a "smooth" type. The former was the typical P. vulgata L., the latter the variety cærulea L. (Jeffreys, 9). It became evident after a little careful observation that the rough type occurred always on rough stones, the smooth type always on polished stones.

I examined some 500 limpets with regard to their habitat, and

I found few exceptions to this rule.

The detailed records are given in Tables VII., VIII., and IX.

Table VII.
Limpets on Rough Stones.

| Stone. | No. of<br>Limpets. | Rough type. | Intermediate type. | Smooth type.      |
|--------|--------------------|-------------|--------------------|-------------------|
| No. 1  | 45                 | 44          |                    | 1                 |
| ,, 2   | 50                 | 42          | 8                  |                   |
| ,, 3   | 55                 | 45          | 10                 |                   |
| ,, 4   | 30                 | 30          |                    |                   |
| ,, 5   | 30                 | 30          |                    |                   |
| ,, 6   | 36                 | 35          |                    | 1                 |
| ,, 7   | 17                 | 17          |                    |                   |
| ,, 8   | 14                 | 11          |                    | 3 (rock polished) |
| Totals | 277                | 254         | 18                 | 5                 |

Table VIII.
Limpets on Smooth Stones.

| No. of<br>Stones. | No. of<br>Limpets. | Rough type. | Composite type. | Smooth type.             |
|-------------------|--------------------|-------------|-----------------|--------------------------|
| e. 35             | 154                | 1           | 7               | 141<br>+5 slightly rough |

 $\label{table IX.} \textbf{Limpets on Stones partly rough and partly smooth.}$ 

| Stone. | No. of<br>Limpets. | Rough type. | Intermediate type. | Smooth type. |
|--------|--------------------|-------------|--------------------|--------------|
| No. 1  | 13                 | 5           | 5                  | 3            |
| ,, 2   | 21                 | 12          |                    | 9            |
| ,, 3   | 16                 | 7           |                    | 9            |
| ,, 4   | 9                  | 3           |                    | 6            |
| ,, 5   | 2                  | 00          | 1                  | 1            |
| ,, 6   | 2                  | 1           |                    | 1            |
| ,, 7   | 4                  | 1           | 2                  | 1            |
| ,, 8   | 3                  | 2           | ·                  | 1            |
| Totals | 70                 | 31          | 8                  | 31           |

The column headed "Composite type" in Table VIII. requires explanation. Certain shells I came across seemed to be rough above and smooth below, showing that they had been rough during the first few months of their life, and had then become smooth. These I called for convenience "composite."

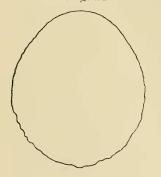
The locality where these data were obtained happened to be

very favourable for the study of the two types of shell. The shore was covered with boulders, some of rough knobby granite, others of smooth polished greenstone. The rough type of limpet occurred on the granite, and harmonised in colour with the greys and browns of the weathered rock. The smooth type occurred on the dark greenstone, and was usually dark in colour. It should

Text-fig. 223.



Text-fig. 225



Text-fig. 227.

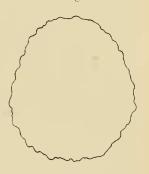


Text-fig. 223.—A typical "smooth" shell. Text-fig. 225.—Outline of margin of same. Text-fig. 227.—Marginal outline of a small "smooth" shell.

Text-fig. 224.



Text-fig. 226.



Text-fig. 228.



Text-fig. 224.—A typical "rough" shell. Text-fig. 226.—Outline of margin of same. Text-fig. 228.—Marginal outline of a small "rough" shell.

be remarked that the smooth type occurs only on very smooth stones, and that for this reason it is not in every locality that limpets are distinctly separable into rough and smooth types. In places where no polished stones are to be found, there are usually no smooth limpets, but only various shades of rough.

The difference between rough shells and smooth shells must be directly due to the difference of the rock surfaces on which they occur, for this is the sole difference between their respective environments. Smooth limpets and rough limpets (on different stones, of course) may be found within an inch or two of one another, and so subjected to environmental influences identical except in one respect. Moreover, since limpets do not wander from stone to stone (Section I.), the difference in environment between rough and smooth shells is constant during their lives. The differences between the two types of shell are therefore caused by the difference in a single environmental factor.

The question arises, in what way does the surface of the rock modify the growth of the shell so as to give rise to two distinct types of shell, according as the surface is rough or smooth? It is necessary first to state in what particulars the two shells

differ.

Differences between the two types.—As stated above, the smooth type corresponds more or less to the variety cærulea L. (the P. cærulea of Linné, S. N. p. 1259), which is thus defined by Jeffreys: "Shell depressed, roundish oval, ribs more delicate and less regular, inside dark blue." It is found "on flat stones and slabs of rock at low water."

The chief peculiarities of the smooth shell are its regular outline, and the number and minuteness of its ribs (text-figs. 223, 225, & 227). When the shell is small, say below 20 mm., there are a large number of fine ribs, 12–14 of these being slightly more distinct than the others. When the shells grow bigger these 12–14 ribs cease to be at all prominent, and the surface becomes covered by small fine ribs, all more or less equal in size. In rough shells, on the other hand, the outline of the rim is irregular, and some of the ribs are much more prominent than the rest (text-figs. 224, 226, & 228). Rough shells of 9–15 mm. in length have only 12–14 ribs. Shells of larger size have these 12–14 ribs, and usually a few more, very prominent, together with minute ribs in between the principal ribs.

Rough shells are usually heavier and thicker than smooth shells, and the thickening of the rim takes place earlier in

them.

The differences between the two types are most evident in medium-sized shells and tend to become obscured in large shells by the effects of weathering and erosion. Small specimens of the smooth type sometimes have their shells gaily coloured with little radiating streaks of white and red and blue, but the general colour of large smooth shells is dark green or brown. Rough shells are coloured in various shades of brown and grey, the ribs being usually tinged with reddish brown.

Effect of Rock Surface on character of Shell.—It is easy to see in a general way that a limpet growing on a smooth surface will

tend to have a smooth shell-rim; for the rim of the shell is kept closely applied to the surface of the rock, and so the deposition of shell-material along the rim is to some extent guided by the surface, and must therefore be even. Similarly, if a shell is kept applied in a definite way to a rough uneven surface, its rim must in growth take on an irregular outline, and certain ribs be emphasised while others are checked in their development.

Now in many cases one can observe in rough limpets that the shell is accurately adjusted to inequalities of the rock to which it clings, or to barnacles on the rock, in such a way that the indentations of the rim between the projecting ribs fit closely round the projecting substances. Two or three cases of this adjustment are given above (Section I.), and a few cases noted by other observers may be adduced here. The phenomenon is in fact

quite common.

Roberts (13) puts on record the following interesting observation of a limpet which he watched returning to its "home." "I watched his course: he arrived, and I immediately perceived a difficulty which he made nothing of, viz., the getting adjusted; he slewed himself round, and fitted a little notch that was in the edge of his shell to a small piece of projecting quartz with wonderful readiness. He was tight in a moment, ready to resist the heaviest breakers or any enemy." The limpet returned daily to the same spot and adjusted himself. Hawkshaw (8) says: "On the top of the smooth fractured surface of a pedestal of flint a limpet had taken up its abode. The shell was closely adapted to the uneven surface which it would only fit in one position." Lukis and Lloyd Morgan record similar cases; and this fitting of the margin of the shell to the irregularities of the rock has been observed also in Acmea spectrum Reeve (Willcox, 15).

An abnormal case which is significant for our purpose is given by Dr. Robertson (14):—"A case once came under my notice of a half-grown limpet that had got jammed between the inequalities of two large stones. It obviously had been there for a considerable time, as the shell had grown into a triangular shape to conform

to the walls of its prison."

The irregular outline of the rim of the rough type of limpetshell is therefore probably a mechanical result of the accurate adjustment of the rim of the shell to the inequalities of the rock on which the limpet grows.

Similarly, the regular outline of the smooth shell is due to the rim being moulded during growth by the polished surface opposed

to it, and hence becoming smooth and regular.

It is a well-known fact that *Anomia* takes the shape of the surface to which it is adherent: if it grows on a *Pecten* shell it bears the impress of the radiating ribs of the *Pecten*. Just in the same way, *Patella*, since it is very sedentary and stays for months adjusted in one definite way to the inequalities of the surface to which it adheres, takes on at the edge of the shell the shape of

that surface; or if the surface be quite smooth, the edge of the shell becomes smooth and regular too.

The difference between the ribs of the two types is to be explained in the same way. All limpets below 15 mm., whether rough or smooth, have about 12 principal ribs. These ribs are very distinct in the rough shell, and project at the rim, giving a very irregular outline to the shell (text-figs. 226 & 228). In the smooth shell these ribs are inconspicuous and hardly project at all, so that the outline of the shell is regular (text-figs. 225 & 227). The specially large ribs of the rough shell arise primarily as projections of the rim, mechanically caused by the irregularities of the rock-surface. These projections of the rim must, owing to the very nature of the shell's growth, be retained during growth, and hence must be continued as ribs. In the smooth shell there is no mechanical formation of projections of the rim, and hence there are no specially prominent ribs.

This case of the rough and the smooth limpet-shell is of interest in that it shows that a small change in an environment may produce through its continuous action a large cumulative result, by a summation of successive little effects. "Continuity" of environment may be apparent only, not real.

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